

*Pterospora* and *Pleuricospora*. The pollen grains of *Allotropa* are three-grooved, while those of *Monotropsis* have two grooves.

Copeland (5) expressed the opinion that *Sarcodes* together with *Pterospora* and *Allotropa* make up the most primitive tribe of Monotropeoideae, being the link between the Ericaceae proper and other Monotropeoideae. The characters of *Sarcodes* as we have come to know them lead us to believe that this is the true conception of the line of evolution.

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## A STUDY OF ISOETES IN SAN DIEGO COUNTY, CALIFORNIA

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Three species of *Isoetes* occur in San Diego County, California: *I. Nuttallii* A. Br., *I. Orcuttii* Eaton, and *I. Howellii* Engelm. To these species, eleven names or combinations of names have been applied at various times and the validity of at least one of them, *I. Orcuttii*, has been questioned by Norma E. Pfeiffer, the most recent student of the genus. (Monograph of the Isoetaceae. Ann. Mo. Bot. Gard. 9: 79-232. 1922.) In the present study ecological and morphological aspects of the genus are emphasized. The writer is indebted to Dr. A. W. Haupt and to Dr. Carl Epling, both of the University of California, Los Angeles, for suggestions.

The living material studied came from the Kearney Mesa which is about fifteen miles north of the city of San Diego and five to ten miles inland, and from a pool about eight miles farther north. This area is a table-land drained by a system of small streams which have running water only after rains. These streams retain occasional pools along their courses, eventually drying up completely during the long rainless period lasting from May until November or December. Between streams are low mounds covered with a chaparral vegetation, alternating with shallow depressions which retain water throughout the rainy season and in which many small hydrophytes flourish. A more detailed account of this region may be found in a recent article by

Edith A. Purer (Ecological study of vernal pools, San Diego County. *Ecology* 20: 217-229. 1939).

Numerous specimens from fourteen localities within the area described were collected at different times of the year. Preserved material, collected in the same region some years previously by Dr. A. W. Haupt and Dr. O. A. Plunkett, was also examined. In addition, types and representative specimens of the following were studied: *Isoetes Suksdorffi* Baker, *I. Nuttallii* A. Br., *I. Orcuttii* Eaton, *I. Howellii* Engelm., *I. nuda* Engelm., *I. melanopoda* var. *californica* Eaton; also representative specimens of *I. Underwoodii* Henderson, the type of which has been destroyed by fire. The following descriptions have been based on the material collected near San Diego.

#### KEY TO SPECIES

Corm 3-lobed; velum complete

Peripheral strands in leaves 3; megaspores frosted and predominantly tuberculate . . . . . 1. *I. Nuttallii*

Peripheral strands in leaves lacking; megaspores usually glossy and predominantly smooth . . . . . 2. *I. Orcuttii*

Corm 2-lobed; velum one-third complete . . . . . 3. *I. Howellii*

1. *ISOETES NUTTALLII* A. Br. ex Engelm., *Am. Nat.* 8: 215. 1874; Pfeiffer, *Ann. Mo. Bot. Gard.* 9: 130. 1922. *I. opaca* Nutt. ex. Engelm., *St. Louis Acad. Sci.* 4: 388. 1882. *I. Suksdorffi* Baker, *Handbook of the Fern Allies* 132. 1887. *Calamaria Nuttallii* Kuntze, *Rev. Gen. Pl.* 2: 828. 1891. *C. Suksdorffi* Kuntze, *l. c.*

Corm 3-lobed; leaves 5-75, mean 21, length 2.5-20 cm., mean 8 cm., spreading, usually with a characteristic twist, stomata numerous, peripheral strands 3, subterranean part of mature leaves occasionally with some brown pigment, velum complete, membranaceous margin up to 5 cm. in length, tapering gradually; megaspores gray (or sometimes white, gray, and dark brown to black within one sporangium), dark brown to black when wet, 260-560  $\mu$ , mean 380  $\mu$ , the markings variable, from distinctly tuberculate to etuberculate on a frosted or occasionally glazed surface; microspores 25-31  $\mu$ , mean 27.5  $\mu$ , tuberculate.

*Isoetes Nuttallii* occupies seepage areas along small streams like those found on Kearney Mesa. In contrast with the other two species, *I. Nuttallii* does not grow where water stands, although the plants may be partially submerged after rains. It was noted in several instances that plants growing in the wetter places were being destroyed by worms and bacteria. The soil in which the plants grow varies from a coarse sand containing a small amount of clay to a clay without sand. Many of the plants are shaded by the chaparral shrubs bordering the streams.

Variation may be observed in (a) number and length of leaves, (b) color, size and marking of megaspores and (c) depth of the

corms in the soil. The number of leaves per plant varies from 5 to 75; their length from 2.5 to 20 centimeters. The plants which have the largest number of leaves are not always the plants with the longest leaves. Most megaspores are gray, but within some sporangia three colors may be found: white, gray, and dark brown to black. When plotted according to size, the megaspores of some individuals produce a bimodal curve. Others have megaspores which, when plotted, produce unimodal curves with small dispersion. Between these extremes are all intermediate conditions, some producing skewed unimodal curves, and some producing less pronounced bimodal curves. The marking on megaspores is variable. Ordinarily they are densely covered with tubercles against a frosted surface. In most sporangia, however, some megaspores usually occur on which the tubercles are wholly or partly suppressed; it is the usual condition for the commissural faces of megaspores to be more prominently marked than the free surfaces. The corms may be covered to a depth of 3 to 4 centimeters or, on the other hand, may be so shallow that the sporangia are visible; all intermediate conditions may be found.

The existence of long-leaved and short-leaved plants, three colors of megaspores in a single sporangia and megaspores which produce bimodal curves when plotted for size may be regarded as evidence of gene mutations.

2. *ISOETES ORCUTTII* Eaton, Fern Bull. 8: 13. 1900; Pfeiffer, Ann. Mo. Bot. Gard. 9: 132. 1922. *I. Nuttallii* var. *Orcuttii* Clute, Fern Allies 253. 1905.

Corm 3-lobed; leaves 3-25, mean 8, length 3-6.5 cm., mean 4 cm., spreading, stomata numerous, peripheral strands none, pigment absent from subterranean portions of mature leaves, velum complete, membranaceous margin 1 cm. or less long, narrow; megaspores gray, dark brown when wet, 220-400  $\mu$ , mean 320  $\mu$ , smooth and glossy, or rarely frosted, sometimes remotely tuberculate; microspores 23-30  $\mu$ , mean 26.5  $\mu$ , tuberculate.

*Isoetes Orcuttii* occupies vernal pools only and is submerged during most of the growing season. After the water evaporates from these pools the plants mature in desiccating soil. In all instances *I. Orcuttii* was found growing in clay soil which is soft when wet and extremely hard when dry.

In contrast to *Isoetes Nuttallii*, *I. Orcuttii* presents very little variation. The leaves exhibit a considerable range in number (3-25) and in this species the larger leaf numbers are associated with the longer leaves. In leaf length the variation is slight (3-6.5 cm.) and does not show the bimodal tendency found in *I. Nuttallii*. The megaspores are uniformly gray with a characteristically glossy surface. Some of the spores have small remote tubercles, and rarely, some of them may be frosted instead of glossy. The megaspores of *I. Orcuttii* are much more uniform in



size than those of either of the other two species. The corms may be covered to a depth of one centimeter at most.

*Isoetes Orcuttii* occupies a different habitat from that of *I. Nuttallii* and differs also in the following morphological characters: the leaves are fewer and smaller and peripheral bundles are absent; megaspores are predominantly glossy and smooth and average approximately 60  $\mu$  less in diameter than those of *I. Nuttallii*. It is evident that although *I. Nuttallii* and *I. Orcuttii* are similar morphologically they differ sufficiently to be considered distinct species.

3. ISOETES HOWELLII Engelm., Trans. St. Louis Acad. Sci. 4: 385. 1882; Pfeiffer, Ann. Mo. Bot. Gard. 9: 139. 1922. *I. nuda* Engelm., l. c. *I. Underwoodii* Henderson, Bot. Gaz. 23: 124. 1897. *I. melanopoda* var. *californica* Eaton in Gilbert, Working List of N. Am. Pterid. 27. 1901.

Corm 2-lobed; leaves 4-56, mean 22, length 5-28 cm., mean 17 cm., spreading, stomata numerous, peripheral strands 4-12, subterranean part of mature leaves usually with abundant dark brown pigment, velum one-third complete, membranaceous margin extending as much as 3 cm. above the soil level and narrowing gradually; megaspores white, tan when wet, 230-600  $\mu$ , mean 430  $\mu$ , usually distinctly marked with a combination of tubercles and distinct and anastomosing crests; microspores 27-39  $\mu$ , mean 34  $\mu$ , tuberculate and occasionally spinulose.

*Isoetes Howellii* is much more widely distributed than either *I. Orcuttii* or *I. Nuttallii*, for while each of these species is strictly limited to a particular habitat as described previously, *I. Howellii* may be found in association with either or may frequently occur alone. It occurs in shallow, quickly drying pools, in pools which retain shallow water and muddy soil, in deeper pools, or in stream beds which are often shaded by chaparral plants. The population of each pool or stream is very limited in area. It is very improbable that the individuals which occupy one vernal pool or stream interbreed with those of another pool or stream. The sporangia are borne too far below ground level for the spores to be blown by the wind and there are no indications that water runs from one pool to another.

The extent to which these differences in environment influence the plants is not known. Nevertheless, there are striking differences between populations of *I. Howellii*. These differences are most evident in the number and length of leaves and the size of megaspores. The first two populations which are summarized in Table 1 exist in two pools which are separated by about fifty feet of higher ground. The first of these is a shallow depression in which the water stands for a short time after rains and, with the exception of *Isoetes* and *Pilularia*, is quite free from plants during the presence of the standing water. In the other pool the

TABLE 1.

Differences between populations of <i>Isoetes Howellii</i>				
	Habitat	Leaf length	No. leaves	Megaspore size
1	partially submerged; not crowded	8-18, mean 14 cm.	14-46, mean 26.5	280-410, mean 350 $\mu$
2	submerged; crowded	10-25, mean 18 cm.	5-20, mean 11	320-480, mean 400 $\mu$
3	partially submerged; not crowded	5-12, mean 8.5 cm.	10-31, mean 17.5	300-450, mean 380 $\mu$
4	submerged; crowded	7-16, mean 11.5 cm.	4-14, mean 8.5	350-600, mean 450 $\mu$
5	shaded	9-18, mean 13.5 cm.	7-26, mean 17	300-580, mean 430 $\mu$

water covers the plants during most of the growing season, since by seepage of water it is kept filled for a longer period. Here the *Isoetes* plants are crowded and are in association with small species of sedges. The differences between these populations are not wholly unexpected. In the widely spaced plants of the first population which grow in shallow water and mud uninfluenced by other plants the leaves are more numerous and shorter than in plants of the second population in which the individuals are crowded and submerged. The size of the megaspores also varies, being smaller by an average of 50  $\mu$  in the plants of the drier more open pool.

Another partially submerged population, Table 1 number 3, which grows several miles from the two just described is made up of individuals about two-thirds the size of the partially submerged plants of the first population. Similarly, another submerged crowded population, number 4, is made up of individuals about two-thirds the size of the submerged plants of the second population, in these the megaspores are decidedly larger by an average of 50  $\mu$ .

The plants thus far considered have been confined to pools. The last population to be considered, number 5, occupies a stream bed and is shaded to a large extent by overhanging chaparral shrubs. These plants differ noticeably from the others by their darker green, more slender leaves. In other characters they are intermediate.

The range in variation in the size of megaspores of individual plants may be very great. Measurements of 400 megaspores from one specimen, indicated a range of from 280-550  $\mu$  a dispersion exceeding those given by Miss Pfeiffer for both *Isoetes Howellii* and var. *minima* Pfeiffer. In morphological characters there is complete intergradation between the species and the variety.

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